The relationship of the fossil fern *Schizaeaopsis* Berry to modern genera in the Schizaeaceae

JUDITH E. SKOG
Biology Department, George Mason University, Fairfax, VA 22030

The fossil fern *Schizaeaopsis* was described by Berry (1911a) as a digitate frond with digitate fertile tips containing trilete, strongly striated spores, but with no information available concerning the structure of the fertile tips. The material was collected from the Lower Cretaceous Patuxent Formation of the Potomac Group, by Fontaine, who had described this fern under the genus *Baieropsis,* in the Ginkqoales (Fontaine, 1889). He included material in two species of *Baieropsis,* since he misinterpreted the sporangial-bearing structures as fungoid growths on the leaves of a ginkgophyte. Berry (1911a) reassigned the material to the family Schizaeaceae in the Pteridophyta, after illustrating that the fertile tips contained fern spores which were similar to spores of *Anemia* and *Lygodium.*

In 1944, O. Selling studied the spores of the Schizaeaceae and excluded *Schizaeaopsis* from any relationship with *Schizaea* because the fossil had trilete spores and those of *Schizaea* were monolete. Selling suggested that the overall fossil morphology indicated that forms similar to *Schizaea* existed in the early Cretaceous but that lack of details about the fertile parts did not allow unambiguous assignment to the Schizaeaceae.

Recently J. van Konijnenburg-van Cittert (1991) accepted the placement of *Schizaeaopsis* within the Schizaeaceae noting that the macromorphology was like that of *Schizaea/Actinostachys* but the spore morphology was like *Mohria/Anemia.*

Reexamination of the fossil fern has elucidated several additional details that influence its placement within the family and suggest possible relationships with modern genera.

MATERIALS AND METHODS

Specimens of the fossil material are from the Paleobotany Collections at the U.S. National Museum of Natural History, Smithsonian Institution, numbers USNM 3209 and USNM 42459. They are from localities near Fredericksburg collected by W. Fontaine. These beds are dated as Upper Aptian in the Lower Cretaceous (Hickey & Doyle, 1977). The specimens were prepared by degagement (removing the rock matrix with fine pointed needles and hairs). Spores were removed from the specimens and mounted on SEM stubs, coated with gold to 40 nm thickness and viewed with a Hitachi S530 scanning electron microscope at a working distance of 15 mm. Spores from the modern species were removed from herbarium specimens and prepared for SEM in the same way. Spore samples for TEM were embedded in LR White epoxy resin following the recommended procedure, sectioned on a diamond knife and viewed with a JEOL 100 C transmission electron microscope. Material (listed below) used in this study was obtained from the pteridophyte collections in the Botany Department, U. S. National Museum of Natural History, Smithsonian Institution.

Actinostachys pennula (Sw.) Hook. *Liesner and Brewer* 15869
Actinostachys subtrijuga Mart. *Amaral, Cornelio, Guedes & Lima* 523
Actinostachys laevigata Mett. *Noumea* 552
Actinostachys melanesica Selling *Smith* 9592

Schizaea pectinata (L.) Sw. *Werdermann & Oberdieck* 416
Schizaea elegans (Vahl) Sw. *Tryon & Tryon* 5292
Schizaea pusilla Pursh. *Fernald & White* 19513
Schizaea dichotoma (L.) Sm. *Hoogland & Craven* 10690

Description

Schizaeaopsis Berry

Annals of Botany, vol. 25, 1911, p. 194

Systematic Paleontology, Lower Cretaceous, Pteridophyta, Maryland Geological Survey, Baltimore, 1911, p. 214.

Schizaeaopsis macrophylla comb. nov.

Baieropsis macrophylla Fontaine 1889, Mon. U. S. Geol. Surv. vol. 15, 1889, p. 212, pl. 90, fig. 6

Baieropsis expansa Fontaine 1889, Mon. U. S. Geol. Surv., vol. 15, 1889, pl. 89, fig. 1

Schizaeopsis expansa Berry 1911, Annals of Botany, vol. 25 p. 194, Textfig. 1, pl. i, figs. 1–6

Schizaeopsis americana Berry 1911, Syst. Paleontol. Lower Cretaceous, Pteriodphyta, Maryland Geol. Surv. Baltimore, p. 214, fig. 2, pl. 22, figs. 1–9.

Emended Diagnosis: Fronds repeatedly dichotomous from the base, veins also dichotomous. Fertile portions oval, mainly apical or occasionally at vein endings along the pinnule margins, fertile tips pinnately divided, sporangia borne along these divisions on both sides of midvein, tightly packed together, annulus apical. Spores tetrahedral, trilete, laesura raised, 50–80 μm in diameter, striated, parallel muri 2 μm wide, occasionally dividing, grooves 0.5 μm wide; spherules of perispore material scattered on surface, fine granular layer of perispore material over surface striations.

Description: The fossil material consists of flattened fronds 6–8 cm long and 4–6 cm wide at the apex that dichotomize several times (Fig. 1, 2 & 20). All bear the fertile tips at vein endings, mainly at the ends of the dichotomous divisions, but these tips are not always all at the same level on the frond (Fig. 3 & 20a). The veins run parallel through the lamina and also occasionally divide (Fig. 4). Veins, or a division from a vein if the fertile tip is below the apex, enter the fertile tips (Fig. 5 & 20b). Unlike the sterile frond segments the fertile tips (3–4 mm long, 1 mm wide) have a central rachis with pinnate lobes (Fig. 6). The pinnate lobes are somewhat folded, due to either maturity or preservation. Removal of the upper layer of folded pinnate lobes reveals that the sporangia are closely packed on the surface of the fertile tips, (Fig. 7), are 0.3–0.5 mm in diam. and have an apical annulus. Spores have been isolated from the sporangia, as noted by Berry (1911b). They are tetrahedral, trilete, have a diameter of 50–80 μm and are ornamented with muri 1–2 μm wide and grooves 0.5 μm wide in the exospore (Fig. 8 & 9). The laesura is slightly raised and often one of the arms is shortened (Fig. 10). The spores have small granular particles (spherules) scattered over the surface; this is the perispore material (Fig. 8–10). The perispore also forms a fine granular layer covering the exospore (Fig. 11).

Type: USNM Paleobotany Collection 3209
Locality: Fredericksburg, VA Patuxent Formation, Potomac Group
Age: Upper Aptian, Lower Cretaceous

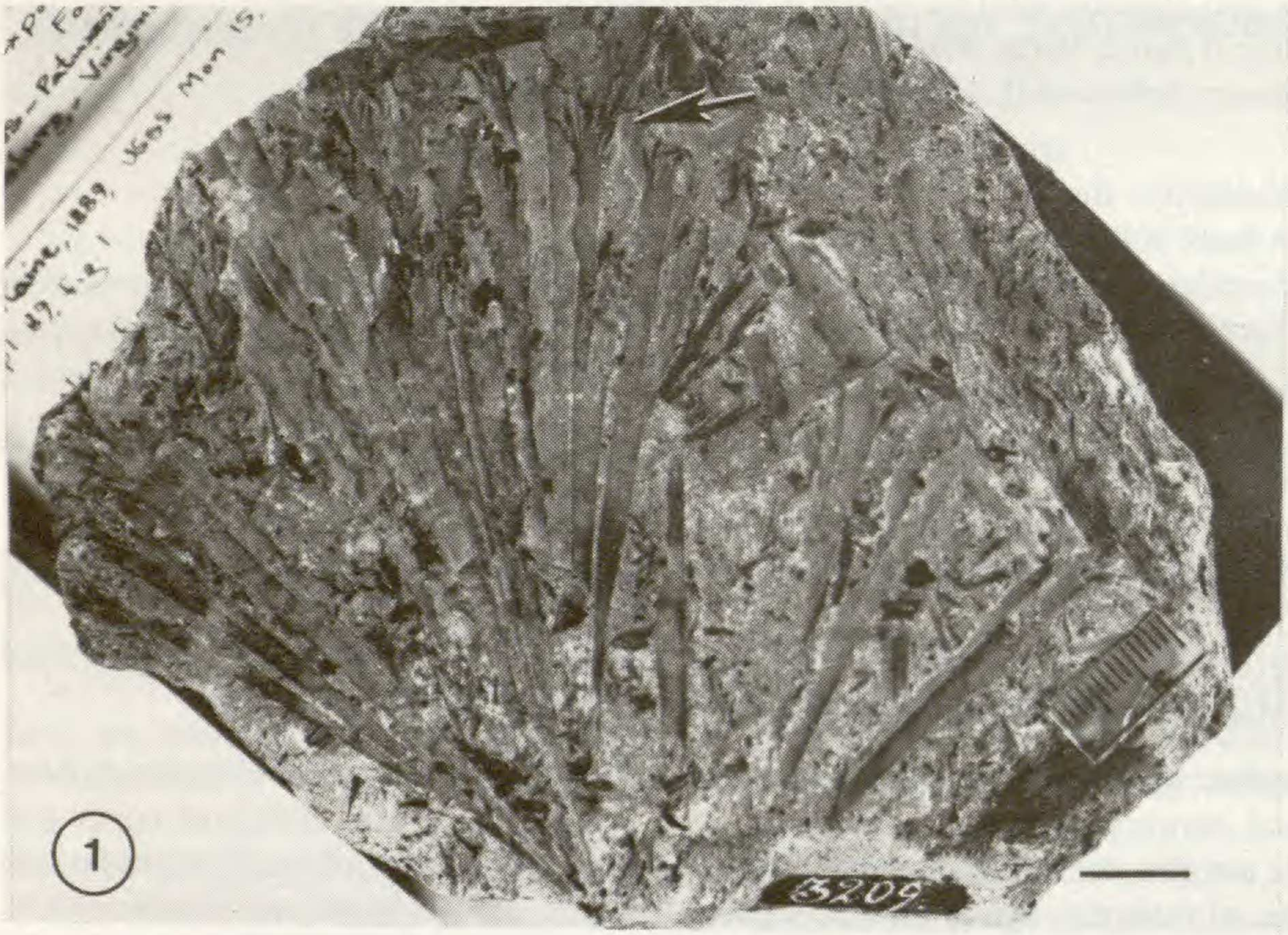

Fig. 1. *Schizaeaopsis macrophylla* USNM 3209. natural size. Dichotomous frond shown with fertile portions at top, arrow indicates one fertile region. Scale bar = 1 cm.

Fig. 2. *Schizaeaopsis macrophylla* USNM 42459. Natural size. Dichotomous frond with one fertile tip shown at left of specimen at arrow. Scale bar = 1 cm.

Fig. 3. USNM 3209 at twice natural size showing fertile tips terminating frond divisions. Although most arise at nearly the same level, some (arrow) are produced at different levels near the tip. Divisions on scale are 1 mm.
Fig. 4. USNM 42459 at twice natural size to show dichotomies and venation of frond. Divisions on scale are 1 mm.

Fig. 5. USNM 3209. One fertile tip of digitate frond portion with vein extending up to fertile division (arrow). Top portion is broken, but most of the fertile divisions attach at nearly the same point. Scale bar = 1 mm.
Fig. 6. One fertile division (USNM 42459) showing pinnate subdivisions (arrow at one). Right side shows pinnate divisions to tip, but left side divisions are folded below into the rock. Scale bar = 0.5 mm.
Fig. 7. USNM 42459 showing sporangia with apical annuli (arrows) over surface of pinnate divisions. Scale bar = 0.25 mm.

Discussion

The genus *Schizaeopsis* was established by Berry (1911a) based on several specimens collected by Fontaine. Fontaine had assigned them to the genus *Baieropsis* (1889) on the basis of the leaf morphology. Fontaine described the sporangia-bearing structures as a fungoid growth on the leaves in the species *B. macrophylla* (USNM 3209 is the illustrated specimen), but made no mention of them on the specimen assigned to *B. expansa* nor is any fertile material of that species illustrated by Fontaine. Berry (1911a) combined *B. macrophylla* with one specimen of *B. expansa* that did bear sporangia (USNM 42459), identified the terminal tips as bearing sporangia and on the basis of the spore characteristics assigned them to *Schizaeopsis* under the name *S. expansa*. Later that year Berry (1911b) noted that "since *Baieropsis expansa* was the type of Fontaine's genus *Baieropsis* it cannot be made the type of the new genus *Schizaeaopsis*", although Fontaine never designated a type for his genus (see Index Nominum Genericorum). Therefore, Berry assigned a new specific epithet, *S. americana*, to the material he had transferred from *Baieropsis*. Since he transferred only one specimen from *B. expansa* and that specimen is distinct from *B. expansa* as described by Fontaine, then the species name should not be *S. expansa*. The specimen illustrated by Berry in his publication is the specimen that Fontaine had identified as *Baieropsis macrophylla*. Berry also transferred all the material Fontaine had originally assigned to *B. macrophylla* to the new genus *Schizaeaopsis*. Thus

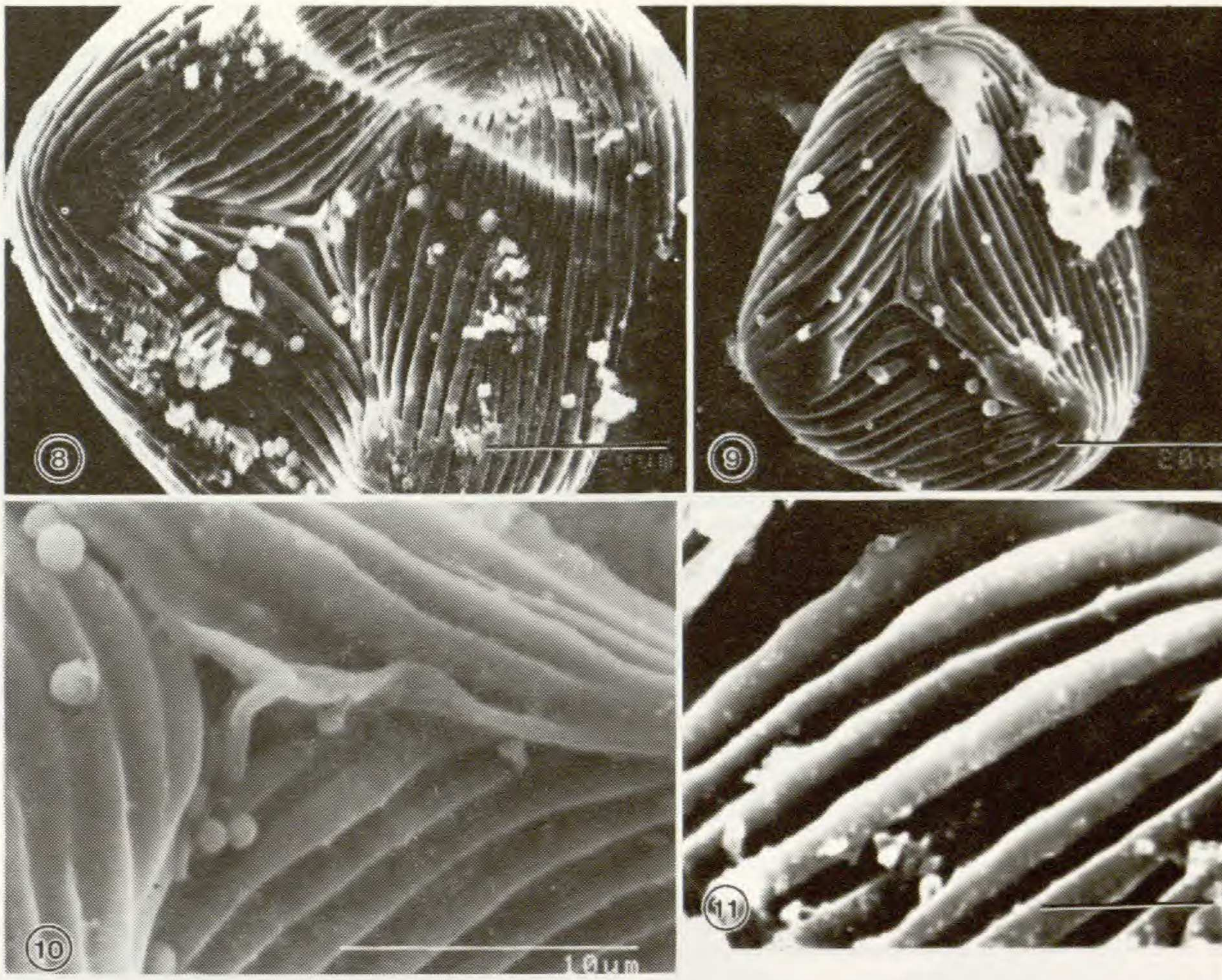

Fig. 8. SEM of spore from USNM 3209. Proximal view of trilete laesura and muri and grooves. Perispore spherules on surface.

Fig. 9. SEM of spore from USNM 42459.

Fig. 10. SEM of spore from USNM 3209 showing shortened arm of the trilete mark, and perispore spherules.

Fig. 11. SEM of muri showing very thin granular layer of perispore on surface of exospore. Scale bar = 0.5 μm.

the older specific epithet available for the material now in *Schizaeaopsis* is actually *S. macrophylla* and the name *S. americana* becomes superfluous. The proper designation is made here, and the type specimen is designated by USNM number (USNM 3209) to clarify the situation.

Comparison with modern ferns clearly indicates relationships to *Schizaea* and *Actinostachys.* The vegetative morphology of *Schizaea* is a digitate frond with a fertile tip on the digitate divisions. In most species there is only one fertile portion on a frond division. Each of the fertile tips is once pinnately divided. In mature *Actinostachys* there is a group of fertile digits on a single frond division attached nearly at a common point (Bierhorst, 1969). Individual digits of *Actinostachys* bear more sporangia than *Schizaea,* in four rows instead of two, and the sporangia are protected by an indusial flap. In *Schizaea* the folding of the pinnate unit protects the young sporangia (Bierhorst, 1969). Bierhorst also suggested that the multipinnate condition of the fertile unit is primitive.

The fossil fern has characteristics of each of the two modern genera. The fertile tips are once pinnately divided and folded over as in *Schizaea,* but there are many fertile digits at the tip of the laminar unit; some are attached nearly at a common point as in *Actinostachys* whereas others may be attached lower down on the lamina. While there is

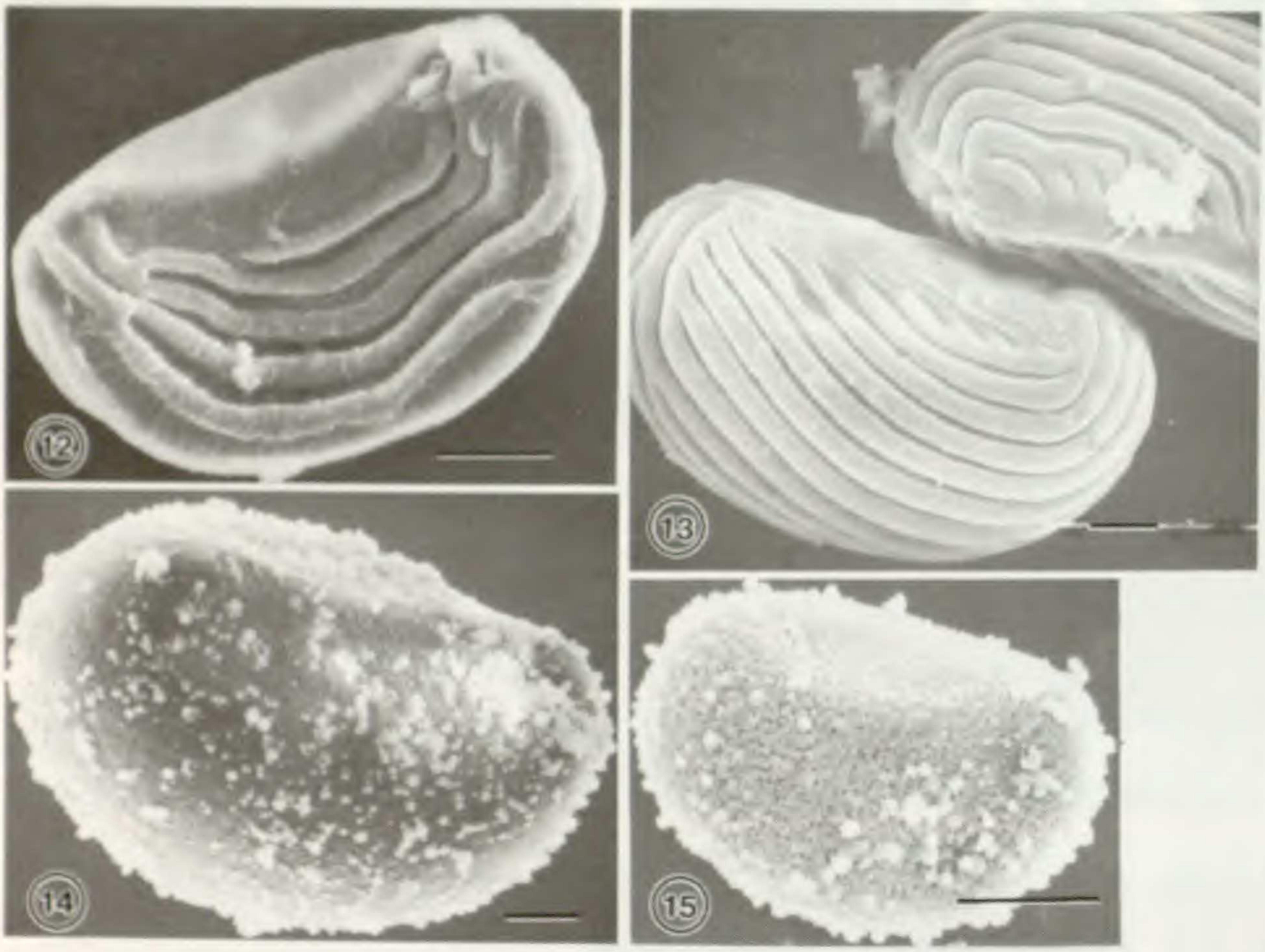

Fig. 12. SEM of spore of *Actinostachys pennula*, Leisner & Brewer 15869. Thin granulate perispore over striate endospore. Scale bar = 10 µm.

Fig. 13. SEM of spore of *Actinostachys subtrijuga*, Amaral, Cornelio, Guedes & Lima 523. Thin perispore with few spherules over striate exospore. Monolete laesura at top. Scale bar = 10 µm.

Fig. 14. SEM of spore of *Schizaea pusilla*, Fernald & White 19513. Granulate perispore with many spherules. Scale bar = 10 µm.

Fig. 15. SEM of spore of *Schizaea elegans*, Tryon & Tryon 5292. Thicker granulate perispore with spherules obscuring exospore. Scale bar = 10 µm.

little question that the frond morphology is similar to the modern genera, the spore morphology is different. Clearly the trilete, tetrahedral, striate spores of *Schizaeaopsis* are closer in morphology to those of *Anemia* subgenus *Anemiorhiza* than to the monolete, reniform spores of *Schizaea* (see Tryon & Lugardon, 1991; van Konijnenburg – van Cittert, 1991). The resemblance of *Actinostachys* spores to those of *Anemia* was noted by Tryon and Lugardon (1991) even though the first is monolete and the latter is consistently trilete. The only trilete spores reported in *Schizaea* are the rare ones in *S. dichotoma* seen by Selling (1944), who excluded *Schizaeaopsis* from any relationship with the modern genus on the basis of the trilete spores, suggesting the fossil form only indicated that *Schizaea* – like morphology had appeared at that time. However, van Konijnenburg-van Cittert (1991) accepted its relationship and uses the evidence from the spores that the earliest spores of this lineage were trilete and striate and monolete spores that are scabrate, granulate and alveolate evolved later.

In an attempt to compare the fossil spores to the modern ones several species of *Schizaea* and *Actinostachys* were examined by scanning and transmission electron

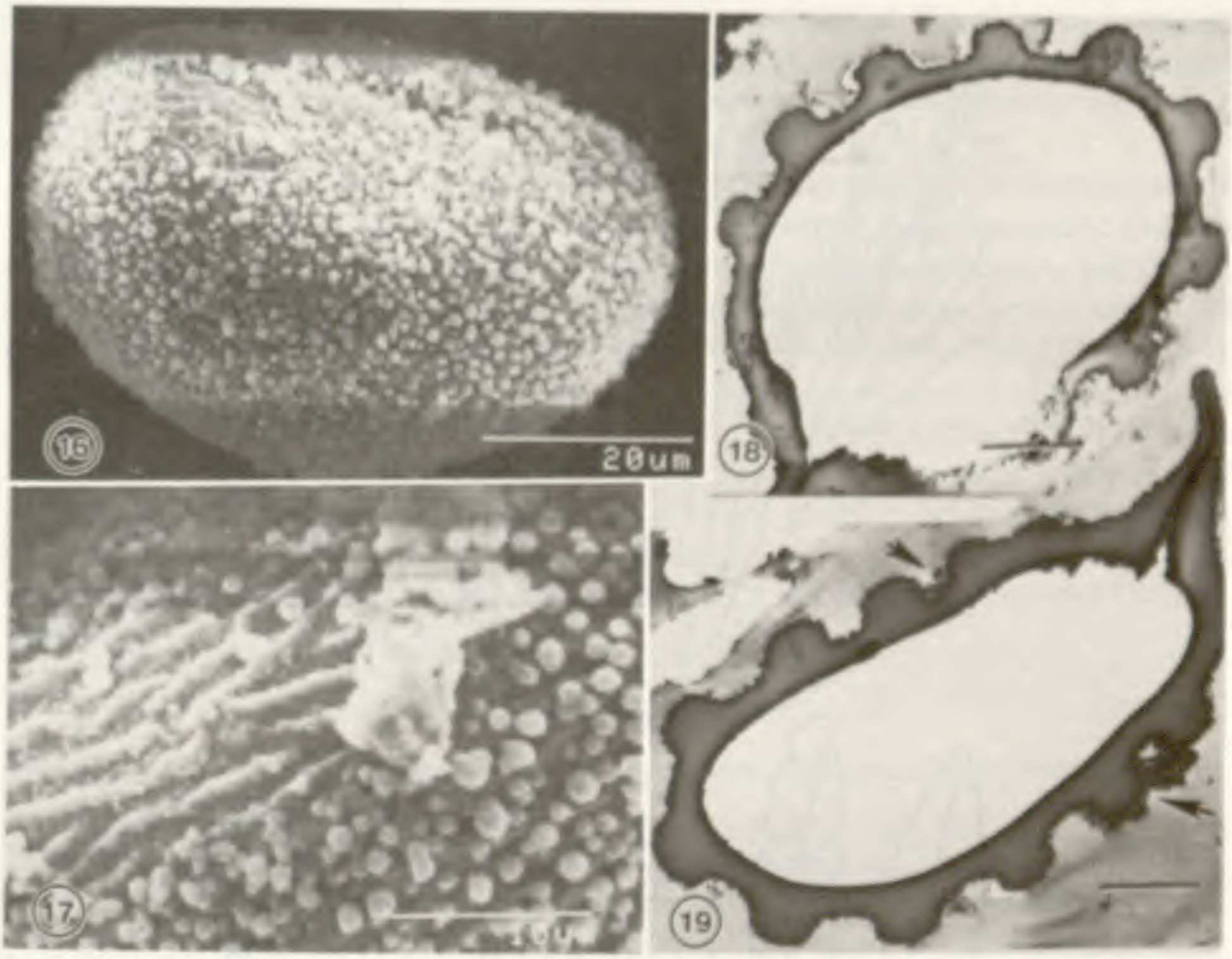

Fig. 16. SEM of *Actinostachys laevigata*, Noumea 552, spore showing granulate perispore on mature spore.
Fig. 17. SEM of *Actinostachys laevigata*, Noumea 552, spore in area where perispore has been removed showing striated exospore below.
Fig. 18. TEM of *Actinostachys pennula*, Liesner & Brewer 15869, showing thick striate exospore and more darkly stained thin perispore (arrow). Scale bar = 0.5 µm.
Fig. 19. TEM of young *Actinostachys laevigata*, Noumea 552, spore showing striate exospore and areas of thickening perispore around and over the grooves (arrows). Scale bar = 0.5 µm.

microscopy. Most of the spores conform to the general observation (van Konijnenburg-van Cittert, 1991) that *Actinostachys* spores have an exospore of parallel ridges and furrows (Fig. 12 & 13) with a thin perispore that is easily removed and *Schizaea* spores have a smooth or more or less granulate exospore with a granulate perispore (Fig. 14 & 15). One species of *Actinostachys*, however, showed a developmental sequence that was particularly informative. *A. laevigata* has spores in the older sporangia that are granular (Fig. 16), but when the perispore is broken away (Fig. 17) the striae are visible below in the exospore. Most *Actinostachys* spores in section show a striated exospore with a thin layer of granulate perispore (Fig. 18). When the spores from the younger sporangia of *A. laevigata* are sectioned the exospore is striate with muri and grooves, as occurs in most species of *Actinostachys*. Gradually deposits of perispore material are laid down (illustrations in Tryon & Lugardon, 1991; van Konijnenburg van Cittert, 1991) and these fill in the grooves and cover the striae (Fig. 19) until the exospore ornamentation is completely covered by the perispore. This developmental sequence suggests that the transition from

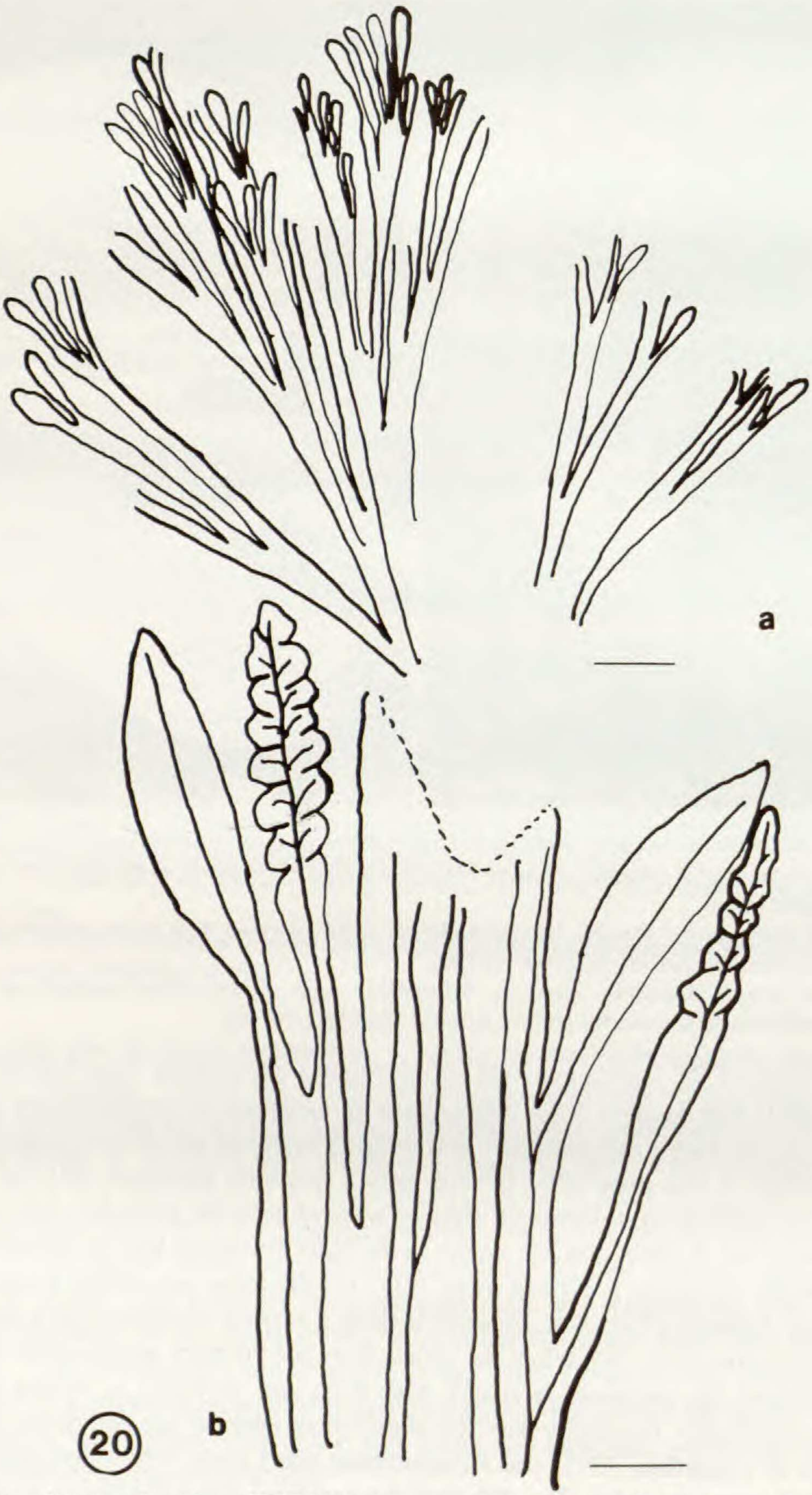

Fig. 20. Line drawing of specimen USNM 3209 showing different levels of fertile tips and dichotomies (a) and an enlargement (b) to show veins and pinnate divisions of fertile tips (see Fig. 5). Scale bars a = 1.0 cm, b = 1.0 mm.

the striate spores to granular spores and then to other modifications is a result of loss of exospore ornamentation and gain of perispore granular material. The exospore is smooth or granulate in extant *Schizaea* (Tryon & Lugardon, 1991), and perispore is very sparse in the fossil spores and in the striate *Actinostachys* spores (van Konijnenburg-van Cittert, 1991).

The fossil fern *Schizaeaopsis* thus combines characteristic spores of *Anemia/Mohria* with frond morphology of *Schizaea/Actinostachys*. During the same time period (Aptian) the first *Actinostachys* – like dispersed spores occur (van Konijnenburg – van Cittert, 1991). The Lower Cretaceous Potomac Group also has fossils belonging to the *Anemia/Mohria* complex and these appear from slightly older beds (Skog, 1987, 1991). They appear to be characterized by more primitive features of *Anemia* according to the character analysis of Mickel (1962) for the genus. The Lower Cretaceous therefore is likely a time of divergence of the common ancestor of *Actinostachys/Schizaea* from *Anemia*. The modern taxa *Actinostachys* and *Schizaea* probably became distinct during the Tertiary. Spores like *Actinostachys* continue from Upper Cretaceous through Paleocene and Eocene, but spores like *Schizaea* first appear in the Miocene (Selling, 1944).

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